



SPATIAL SOUNDSCAPE ECOLOGY:

Application in a Paleotropical Rainforest

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Mentors



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Abstract

The world's biodiversity is declining with much of the decrease attributed to human activity. The paleotropical rainforests of Borneo contribute 10% of the world biodiversity but are at risk of destruction due to logging and other human interests. Soundscape ecology, defined as the study of the composition of sounds in an environment, is a new field that offers solutions for assessing biodiversity and disturbance. Spatial dynamics are an important component of an ecosystem, yet the link between spatial dynamics and soundscapes has not yet been studied. It should be possible to assess disturbance of an ecosystem by analyzing the spatial structure of the soundscape. Particularly, soundscapes in undisturbed ecosystems should exhibit more spatial autocorrelation than soundscapes in disturbed ecosystems. We took automated bihourly 10-minute recordings at a disturbed ($n = 4,905$) and an undisturbed ($n = 8,450$) transect in Brunei, Borneo, for a month-long period. Sites had identical spatial configurations, with 13 recorders at each site. Alpha acoustic indices were computed from recorded sound files, and beta acoustic indices were calculated pairwise for each 13 recorder group at each unique recording time. Moran's I statistics were calculated to compare the resultant alpha indices from the two transects. We compared beta indices by Mantel Tests. Spatial statistics on alpha and beta indices reveal more spatial autocorrelation and correlation at the undisturbed site. Of all alpha indices, Normalized Difference Soundscape Index (NDSI) detected spatial autocorrelation to the highest extent. Beta acoustic indices detected differences between the two sites more precisely, due to their comparative nature.

VanSchaik, J. (2017). Spatial soundscape ecology: Application in a paleotropical rainforest. *Journal of Purdue Undergraduate Research*, 7, 65–71. <https://doi.org/10.5703/1288284316399>

Keywords

paleotropical rainforest, soundscape, spectrogram, soundscape ecology, acoustic index, spatial autocorrelation, Moran's I , Mantel test, biodiversity

INTRODUCTION

Human activity is altering the biodiversity of our planet, which may in turn alter ecosystem processes and have an economic impact on society (Chapin et al., 2000; Costanza et al., 1997). It is becoming increasingly important to understand and quantify biodiversity in a robust and timely manner (Balmford, Crane, Dobson, Green, & Mace, 2005). Traditional biodiversity measurements require many resources, specialist time, and may disturb existing landscapes (Cranston & Hillman, 1992; Wilkie, Mertl, & Traniello, 2007). Therefore, rapid biodiversity assessment with noninvasive methods and low operational costs may be preferable.

When studying biodiversity, ecological processes exhibit various forms of spatial heterogeneity. In particular, organisms in an ecosystem tend to exhibit patchy or gradient spatial structure (Legendre & Fortin, 1989). Animal communities are spatially structured at many scales and comprise a community composition. These community compositions can be compared, as well, by assessing spatial variation. These structures allow researchers to understand trends and the influence of ecological processes in a geographic region over time. One aim of spatial analysis is to discriminate between these sources of variation. Many times, events such as disturbances, may influence the structure of a community (Borcard, Gillet, & Legendre, 2011).

Ecologists are concerned with how anthropogenic disturbances affect biological richness and the soundscape of an environment (Pijanowski, Farina, Gage, Dumyahn, & Krause, 2011). A soundscape is defined as the composition of sounds in an ecosystem (Pijanowski et al., 2011b). Soundscape ecology is a new field that is interested in assessing relationships between biodiversity and the soundscape. (Pijanowski et al., 2011a). Important tools for assessing such relationship are acoustic indices, which are implemented to measure ecologically meaningful information in a sound recording (Sueur, Farina, Gasc, Pieretti, & Pavoine, 2014). Research into the relationship of acoustic diversity and biodiversity have used acoustic indices to successfully quantify biodiversity (Gasc et al., 2013a; Obrist et al., 2010; Sueur, Pavoine, Hamerlynck, & Duvail, 2008a; Towsey, Wimmer, Williamson, & Roe, 2014). Ecological indices that are responsive to biodiversity should be responsive to the spatial gradients, assuming that species exhibiting spatial heterogeneity are vocalizing. Landscapes support varied animal community diversity due to geographic location and habitat, with some landscapes having a higher level

of sound diversity (Diwakar & Balakrishnan, 2007; Riede, 1993). Borneo is home to the one of the most biodiverse rainforests in the world with a highly active and acoustically rich soundscape (Pekin, Jung, Villanueva-Rivera, Pijanowski, & Ahumada, 2012). Researchers believe that species in undisturbed regions of this rainforest have stabilized into local spatial niches while species in disturbed regions may have abandoned their natural niches (Schmidt, Römer, & Riede, 2013). This phenomenon may be due to ecological niche differentiation and acoustic competition, whereby communication space is partitioned among species (Pijanowski et al., 2011b; Schmidt, Römer, & Riede, 2013). Spatial analysis may provide evidence for differentiation between undisturbed and disturbed regions.

Currently, the efficacy of ecological indices for assessing ecological spatial autocorrelation has not yet been tested, yet one goal of soundscape ecology is to quantify spatiotemporal patterns of soundscapes (Pijanowski et al., 2011b). In this study, we applied the tools of soundscape ecology in a novel way: (1) Which acoustic indices are more responsive to spatial structure? and (2) How does the level of spatial autocorrelation vary between an undisturbed and a disturbed region of a paleotropical rainforest? Borneo is home to the oldest and most biodiverse rainforests in the world. This rainforest has a highly active and acoustically rich soundscape (Pekin et al., 2012). Species in undisturbed regions of the rainforest have stabilized into local spatial niches (Schmidt & Balakrishnan, 2015), while species in disturbed regions may have abandoned their natural niches. Vocalizing species partition frequency space to avoid competition (Pijanowski et al., 2011b; Schmidt et al., 2013). We therefore hypothesize that in the undisturbed, old growth region of the rainforest, species will exhibit well-defined acoustic niches, whereas in the disturbed region these acoustic niches may change or no longer exist. Here we mean *disturbed* to mean that the study site had recently been exposed to logging and *undisturbed* to mean that the site was old growth forest devoid of human activity. We conjectured that the level of spatial autocorrelation will be higher in an undisturbed region.

MATERIALS AND METHODS

Study Sites

The study was conducted at two sites near Kuala Belalong Field Studies Center in Brunei on the island of Borneo in Southeast Asia. The old growth forests in the three-acre study plot are 300 million years old with over 70 species of frogs and toads and 32 cicada species. Samples were collected as sound

recordings using SM2+ acoustic recording units with a sample rate of 44,100 Hz, stereo. This recording interval provided 48 recording times that could be studied independently. Sound recordings ($n = 8,450$) were collected from an undisturbed transect (T2) at 13 spatially unique sites from February 13 to March 7, 2014. Sound recordings ($n = 4,950$) were also collected from a disturbed transect (T3) at 13 spatially unique sites from March 3 to March 15, 2014. At each site, 10-minute recordings were taken every 30 minutes. Note, the sample sizes for T2 and T3 differ, and a confounding variable may be a change in soundscape dynamics due to yearly seasonality. However, T3 recordings were taken after T2 recording in the same season. T2 and T3 recorders shared identical spatial arrangements. The spacing was designed to optimize redundancy across multiple distance lags.

Index Calculation and Preliminary Analysis

Alpha Acoustic Indices (ACI, ADI, AEI, Bioac, H , H_p , H_r , M , and NDSI) and beta acoustic indices (D_t , D_{cp} , D_p , dw , KLD , $KLD1$, $KLD2$, KSD , KSF , LS , and SS) were calculated on the first 60 seconds of all T2 and T3 recordings using the R package *seewave* (Sueur, Aubin, & Simonis, 2008). See Table 1 for index acronyms.

Preliminary analysis of variance (ANOVA) tests indicate that the Bioac index varies significantly between the T2 and T3 site ($p < 2e-16$) and vary significantly at 46 of 48 recording times (Bonferroni corrected $p < 0.00104$). Notice, ANOVA assumptions are violated by temporal correlation, although regressing the Bioac index produces normal residuals. For each index, index distribution depended on transect for at least one recording time (Kruskal-Wallis nonparametric rank sum test, Bonferroni corrected $p < 0.00104$). This provided a reference when analyzing alpha and beta indices using statistical tests. Moran's I was used to compute the spatial autocorrelation of each alpha index for both aggregate time and individual time points. Mantel tests were used to assess correlation between spatial distance and soundscape difference via beta indices.

Compute Mean Spectrum

For each recording, spectrograms (Hanning window length = 512 samples) were generated from the first minute of each file. The mean sound power for each frequency bin was calculated to produce a mean spectrum vector. The mean spectrum vectors were grouped by recording time and transect and averaged across frequency bins. This produced a plot, the mean mean spectrum that depicts an average day in

ACI	Acoustic Complexity Index
ADI	Acoustic Diversity Index
AEI	Acoustic Evenness Index
Bioac	Bioacoustic Index
H	Composite Entropy
H_f	Spectral Entropy
H_t	Amplitude Envelope Entropy
M	Median of Amplitude Envelope
NDSI	Normalized Difference Soundscape Index
D_t	Temporal Dissimilarity
D_{cf}	Cumulative Dissimilarity
D_f	Spectral Dissimilarity
Dw	Difference Between Waves
KLD1, KLD2, KLD	Kullback Leiber Divergence ($A \rightarrow B$, $B \rightarrow A$, and symmetric)
KSD, KSF	Kolmogorov Smirnov Distance
LS	Log Spectral Distance
SS	Spectral Similarity

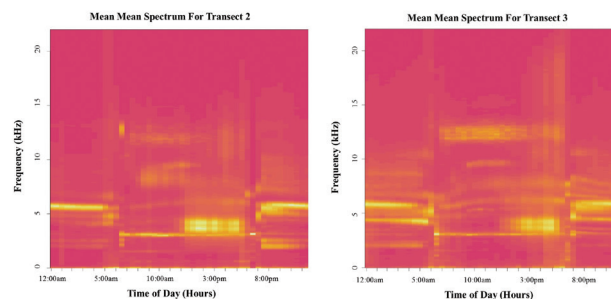
■ **Table 1.** Acronyms for acoustic indices.

the soundscape of the two sites (see Figure 1). The T2 and T3 mean mean spectrum plots allow for a preliminary comparison of a daily cycle of the soundscapes at these sites.

Spatial Analysis

Moran's I was used to compute the spatial autocorrelation of each alpha index for both aggregate time and individual time points. Moran's I is a widely used assessment of spatial autocorrelation in ecology (Legendre & Fortin, 1989). Spatial correlation measures how observations in space have similar (positive correlation) or dissimilar values (negative correlation) compared to randomly selected pairs. A process or pattern that varies across an area is spatially heterogeneous. The magnitude and extent of spatial correlation can be tested with a Moran's I test (Borcard, Gillet, & Legendre, 2011). We computed the distance matrix using inverse square weights for the spatial in calculating Moran's I. This weighting system was chosen because sound propagation is modeled by the inverse square law and is commonly used in ecological studies.

Mantel tests were used to assess correlation between spatial distance and soundscape difference via beta indices. The Mantel test is a statistical test often used in ecology to assess species environment



■ **Figure 1.** Mean mean spectrum plots of T2 and T3. Y axis units are frequency in kHz. X axis units are standard American military time.

relationships (Legendre & Fortin, 1989; Legendre & Legendre, 1998). The test calculates correlation between two distance matrices and then permutes the columns to create a bootstrap distribution which can then be used to generate a test statistic. The test statistic can be used to accept or reject the null hypothesis of no element-wise correlation between the matrices. We calculated beta indices on T2 and T3. Beta indices are a class of acoustic indices that attempt to quantify an ecological difference between two recordings. For a given time, the ij^{th} entry in the beta index matrix corresponds to the average beta index comparing the recording from sensor i with the recording from sensor j . The ij^{th} entry of the distance matrix simply corresponds to the euclidean distance between the sensor i and sensor j .

RESULTS

A Moran's I value was calculated for each index in T2 and T3 using 13 unique spatial points for each recording time. We computed 95% bootstrap confidence intervals of the mean Moran's I value for each acoustic index (see Figure 2). For each individual Moran's I value, an approximate 95% confidence interval was generated under the null hypothesis of no spatial autocorrelation (see Figure 3). The distributions were slightly skewed due to Moran's I being averaged across different sampling times. Overall, there were four types of responses from the 95% bootstrap test. The first type included acoustic indices ACI, ADI, and AEI. This group did not reveal significant discrimination in spatial autocorrelation between sites. The second type included H_t and M, whose confidence intervals were close to zero. The third type included Bioac, H, and H_p , all similarly anomalous as confidence intervals appear to reveal significant spatial autocorrelation. In this group, T3 has higher spatial autocorrelation values, contrary to expected. The fourth type included NDSI and showed the average Moran's I value was significantly above zero for both sites, with the T2 interval much

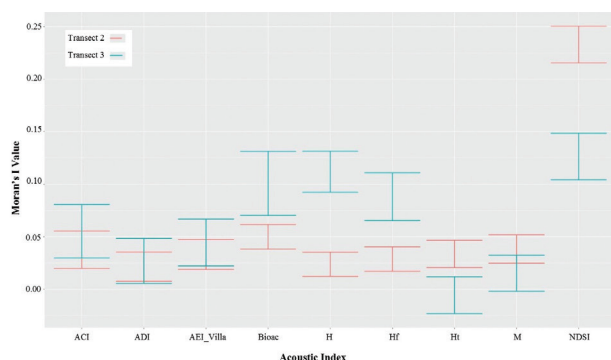


Figure 2. Bootstrap 95% confidence intervals for mean Moran's I for each index at T2 and T3.

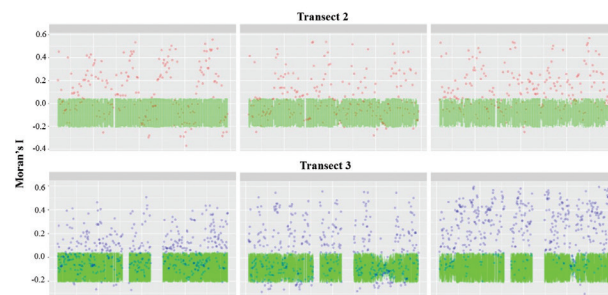


Figure 3. Approximate 95% confidence intervals for Moran's I of NDSI, Bioac, and ACI for every recording time for T2 and T3.

index	D _{cf}	D _f	D _t	dw	KLD	KLD1	KLD2	KSD	LS	SS
T2 Reject Rate	0.7708	1.0000	0.0000	1.0000	1.0000	1.0000	1.0000	0.9792	1.0000	0.0000
T3 Reject Rate	0.3542	0.9792	0.0000	0.7083	0.9583	0.9583	0.9375	0.4792	0.9583	0.0000

Table 2. Rejection rates for Bonferroni corrected ($\alpha = 0.05$) Mantel test for each recording time. We see that for all beta indices, the rejection rate in T3 is lower than or equal to the reject rate T2.

higher than T3. This indicates that there was significant spatial autocorrelation of NDSI at both sites, but to a much higher extent at T2. As seen in Figure 3, there is a relatively large percentage of the NDSI values for T2 that lie outside of the confidence intervals while other indices there are relatively more values within the confidence intervals. This confirms the aggregate results depicted in Figure 2 but on a finer level. Comparing with the T3, a relatively higher proportion of points fall in the confidence intervals further confirming the prior results.

For each beta index, a Mantel test was performed using the 78 (13 choose 2) unique pairs of recorders. For each site, index and recording time beta index matrices were averaged across every sampled day. This produced a Mantel test statistic and significance level (permutations = 9999, $\alpha = 0.05$), under the null hypothesis of no spatial correlation, for each site, index, and recording time combination. After a Bonferroni multiplicity correction, the null hypothesis rejection rate across different recording times was calculated. We will from now on refer to these as the average beta index Mantel test results, which are summarized in Table 2. We can see that for every index. The T3 rejection rate was less than or equal to the T2 rejection rate. This implies that for any beta index, there were equal to or fewer recording times that showed significant autocorrelation. We see that D_t and SS have a 0 reject rate for both transects, implying that average beta index Mantel tests for

these indices never detected any spatial correlation. D_p , the KLD beta indices, and LS Mantel tests have a high reject rate for both T2 and T3, implying spatial correlation for most recording times in these sites. D_{cf} , dw, and KSD offer the most discrepancy in reject rate between T2 and T3.

DISCUSSION AND CONCLUSION

Firstly, preliminary results via ANOVA, nonparametric distribution comparison, and visual inspection of mean mean spectra indicate that the soundscapes of T2 and T3 were different (see Figure 1). The restructuring of different frequency bins and time in the mean mean spectrum indicate a difference in species composition between the two sites. Based on our hypothesis, we should, therefore, expect the spatial structure of the soundscapes to differ as well.

Of all the alpha indices tested using Moran's I, NDSI was most responsive to spatial autocorrelation. NDSI is a compositional index that calculates the spectral amplitude ratio between frequency bands. In Borneo, where niche composition can vary on a small scale, NDSI should be expected to deliver this result. NDSI may be adaptable to measuring spatial autocorrelation in different environments because frequency bins can be adjusted to ecologically relevant bins for that ecosystem. The results suggest that acoustic indices sensitive to spatial autocorrelation should utilize a frequency bin ratio. A distance matrix of

all possible spectral amplitude ratios could be used as a multivariate index, compounded to produce a univariate index. Currently there is not a widely accepted multivariate soundscape index, but such indices could be useful input for classification methods such as artificial neural networks and support vector machines. The Moran's I bioacoustic values for T3 stand out in Figure 3 as they show a clear daily trend in spatial autocorrelation, whereas the T2 values do not. There could be several reasons for this. First, there might also be a daily trend for T2 that was obfuscated by a larger sample size. Secondly, of all the indices, bioacoustic seemed to be the most responsive to daily seasonality in this set of recordings.

The results in Table 2 agree with our hypothesis of more spatial autocorrelation in T2. Indeed, a disturbance regime induced changes in species composition, biodiversity, and spatial structure, which was reflected in the spatial structure of the soundscape. To understand which beta indices are more responsive to spatial structure, we should consider how these indices are calculated. D_p , which indicated no spatial structure whatsoever, is a measure of amplitude envelope dissimilarity. The amplitude envelopes could be easily skewed by one nearby acoustic source. For example, in Borneo alone, cicada may fly close to the microphone for part of the recording. SS is calculated using only minimum and maximum values of a mean spectrum, which leaves out compositional information from the remaining frequency bands. The KLD family of beta indices calculates the Kullback-Leibler divergence between two frequency spectra. D_f calculates dissimilarity between frequency spectrum, and LS calculates log spectral differences. As they are spectral dissimilarity measures, KLD, KLD1, KLD2, D_p , and LS all show a similar result: that there were only a few times in which T3 was not spatially autocorrelated. Looking at our mean mean spectra, this makes sense. The composition was different in a relatively small proportion of frequency bins, although it differed between T2 and T3 at almost all times of day. Spectral dissimilarity measures are effective for measuring spatial structure. They may be even more effective in environments where vocalizing species occupy larger bandwidths. D_w incorporates both spectral and temporal differencing measures, while D_{cf} calculates cumulative spectral dissimilarity. These two indices detect spatial structure, but not as saturated as the spectral dissimilarity beta indices. Therefore, these indices could be used to robustly test spatial structure in other paleotropical soundscapes.

The common theme between alpha indices and beta indices that detect spatial structure seems to be

spectral composition. Soundscape ecologists have been using the frequency spectrum to estimate biodiversity (Pijanowski et al., 2011b). They should continue to do so, as these results indicate that indices based on spectral composition respond best to changes in soundscape spatial structure brought upon by changes in biodiversity.

Index calculations similar to the above could run at different index defaults (this may vary for each environment). The method could also be improved by using different values for the spatial weight matrix. Work is being done to model acoustic propagation in several different environments (Graupe, 2017), which may provide insight into how weighting values may differ for other environments.

There are other methods that could be used to determine spatial structure in a multiple recording environment, such as sound-source localization. This could be used to approximate spatial positions of sound sources. This idea was entertained for the Borneo data; however, several challenges arise. Firstly, source localization in a noisy environment is difficult to assess. In an acoustic environment as rich as Borneo, separating one signal from hundreds of different vocalizing species is difficult, which becomes apparent when examining cross-correlation and autocorrelation functions of audio files.

We might benefit from an even more controlled study. One approach is a lab-controlled soundscape where actual spatial autocorrelation of sound sources are known. Another approach would be able to use simulation methods to generate soundscapes along a controlled spatial autocorrelation gradient. A promising method for generating realistic soundscapes is cellular automata, which is already used in ecology to generate spatial datasets (Wolfram, 2002; Baltzer, Braun, & Köhler, 1998).

This study was done in a paleotropical rainforest. Other indices may perform better in other environments. Soundscape data is inherently time series data. In the future, it may be beneficial to assess future studies with spatiotemporal models.

ACKNOWLEDGMENTS

Thanks to Kristen Bellisario for mentorship and guidance, to Amandine Gasc for mentorship, and ideas, to Dr. Bryan Pijanowski for mentorship and data collection, to Mark Ward and the Stat LLC for making the learning happen. This material is based upon work supported by the National Science Foundation under Grant No. 1246818.

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